

## Diversity and structure of pelagic copepod populations in the frontal zone of the eastern Alboran sea

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### Abstract

During the oceanographic campaign, ALMOFRONT I (April 24–May 26, 1991) a total of 50 vertical zooplankton hauls was carried out in the Alboran Sea using a triple net. Leg A (18 stations; 18 hauls) described a widely spaced grid in the region of the Atlantic current and some northern eddies, while Leg B (16 stations; 32 hauls, 6 hydrodynamically characterized sites sampled during a two day period) covered a more restricted area in the frontal zone. Ninety-one species of copepods were found in 100 samples collected by either 200  $\mu\text{m}$  or 500  $\mu\text{m}$  mesh size nets, including 32 genera and 26 families. Copepod abundance, structure indexes (species richness, evenness, Shannon species diversity index, standardized for unequal sample counts) and species abundance patterns (as rank-frequency diagrams) are presented and compared among the sites of leg-B. Copepod abundance was found to be the highest in the more productive sites of the Atlantic current. Structure indexes values and the changing shape of rank-frequency diagrams give a coherent view of the ecological succession stages of the copepod community. Juvenile stage (1) develops from the Atlantic divergence zone, left side of the jet. More mature stages (1' and 2) occur on the right side of the jet influenced by cross frontal flow. Both abundance and structure indexes decrease within an anticyclonic gyre south to the current. A situation more influenced by oligotrophic conditions was observed in a Mediterranean anticyclonic gyre north of the current. The importance of lateral displacement and meandering of the Atlantic current across the Alboran Sea to the community structure is discussed.

### Introduction

Populations of copepods represent a dominant component of the mesozooplankton biomass in oceanic zones. They are composed principally of herbivorous and omnivorous species, carnivorous ones becoming progressively more important in oligotrophic systems. In regions influenced by the presence of fronts (Sournia *et al.*, 1990), copepod distribution and abundance appear closely linked to the hydrological structure. A great diversity of hydrological structures was encountered in the Alboran Sea (western Mediterranean Sea) during the ALMOFRONT-1 survey (Prieur *et al.*, 1993). Frontal zone, and eddies are related to the meandering Atlantic current, which enters the Mediterranean by the Strait of Gibraltar. The area covered by the survey thus appeared especially suitable for an investigation of the relationships between physical conditions and

zooplankton populations. In the Alboran Sea, investigations of copepods have concentrated principally on the establishment of faunal lists. Massuti and Navarro (1950) compiled a species list, with indications of abundance. The work of Giron (1963) has long served as an important reference. She listed 72 species of 41 genera and estimated their relative abundances. Subsequently, Duran (1970), Vives *et al.* (1975) and Greze *et al.* (1985) complemented the faunal list, which now stands at 286 known species. Certain species are indicators of Atlantic water and are not found east of the Alboran Sea.

The copepod assemblages of the eastern Alboran Sea, determined by nets of two mesh sizes, will be briefly presented. Variations of copepod population abundances across the different hydrodynamical compartments of the Alboran Sea will be discussed, as well as the rank-frequency diagram shapes and population

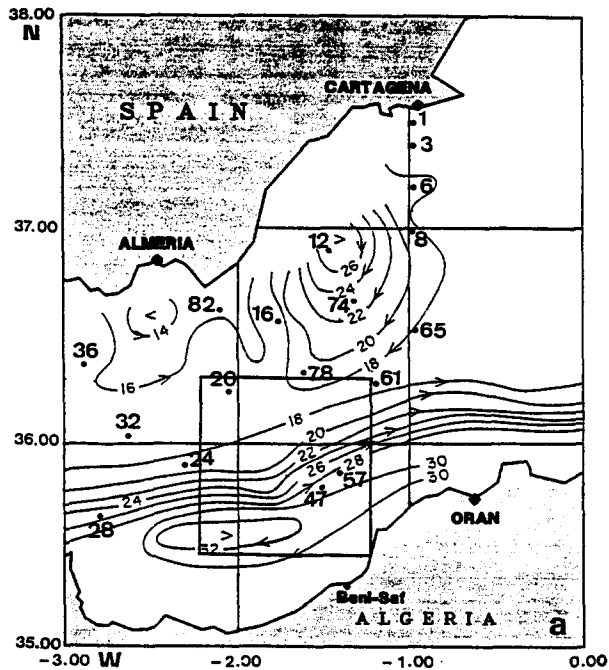


Fig. 1 A. Locales of the stations during Leg A superimposed on the dynamic topography of the surface (in cm. dyn.), relative to the 400 dbars level (modified from Prieur *et al.*, 1993).

structure index values standardized by count number, as species richness, species diversity and evenness.

### Material and methods

The 'ALMOFRONT-1' survey was designed to study the effects of the Atlantic current on plankton production (April 24 – May 26, 1991) Prieur *et al.* (1993). An atlas of the data recorded during the cruise will be soon published as a collective work (L. Prieur & A. Sournia, editors, in preparation). ALMOFRONT-1 was divided in two legs (Fig. 1a). During Leg-A, a grid of CTD casts was used to map the mesoscale hydrological structure of the eastern Alboran Sea. During Leg-B the ship visited six typical sites across the frontal area. In each site the ship followed close behind a line of free-drifting sediment traps during a 2-day period (Fig. 1b). A WP2 triple net (500  $\mu\text{m}$ , 200  $\mu\text{m}$  and 80  $\mu\text{m}$  mesh size, 0.25 m<sup>2</sup> surface aperture each, Razouls & Thiriou, 1973) was used to sample zooplankton. In total, 50 vertical hauls were made at 34 stations, (18 during Leg-A, and 16 during Leg-B). Samples were fixed on board in 3% buffered formaldehyde.

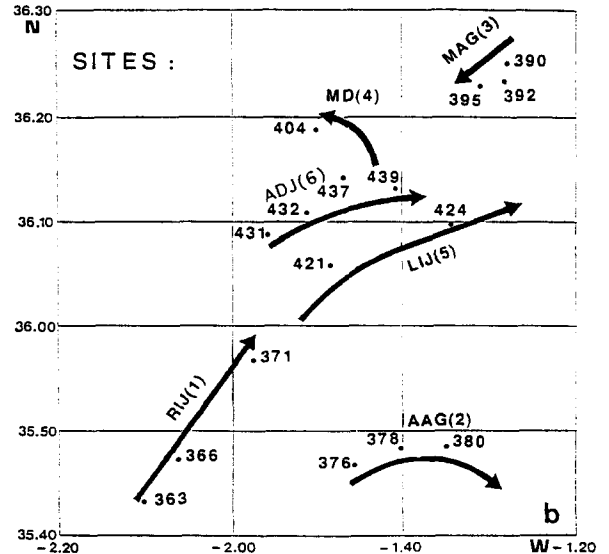


Fig. 1 B. Localization of the zooplankton hauls at the six sites during Leg B (see text or Table 1 for an explanation of the abbreviations used for sites). The curved arrows show the two-day period drifts of free sediment traps (modified from Prieur *et al.*, 1993).

During Leg-A, 200 m-surface plankton hauls were taken at some widely spaced CTD stations situated mainly in the zone of the Atlantic current and in two northern eddies (Fig. 1a). During Leg-B, hauls were made over three depth ranges: (a) 100–0 m; (b) 200–100 m; (c) 200–0 m at each site. Later in the text we use the letters a, b and c, following the station number, to specify the depth strata of the plankton haul.

Following Prieur *et al.* (1993, table 1, page 82), the stations visited during leg A can be located within the different hydrodynamic mesoscale structures of the Eastern Alboran Sea using a dynamic height map (Fig. 1a). The sites visited during leg B could be more easily characterized by their hydrodynamic situation, taking into account CTD and ADCP measurements. The sites were chosen to describe the cross frontal hydrological structure and were ranked according to the depth of the isopycnal 1028 kg/m<sup>3</sup> which decreases from the south to the north as follows:

- Site 2: southern Atlantic water anticyclonic gyre, AAG(2) site code, stations 376, 378a and b, 380 a, b and c.
- Site 1: right inside part of the jet of the Atlantic current, RIJ(1), stations 363, 366 and 371a and b.
- Site 5: left inside part of the jet, near the zone of maximum ADCP measured current speed (0.6 m/s mean surface velocity) and of convergence, LIJ(5), stations 421a and c and 424a and c.

– Site 6: ADJ(6) is an Atlantic water divergence zone on the left edge of the jet, stations 431a and b, 432a and b, 437a and b and 439a and b.

– Site 4 left outside of the jet, in Mediterranean water, may represent a divergence zone with a weak (0.1 m/s) westward current, MD(4), stations 404a,b and c.

– Site 3 represents an area where the influence of Mediterranean water is most marked, and situated near the periphery of an anticyclonic gyre, MAG(3), stations 390a, b and c, 392a and b, 395a and c.

Plankton hauls were taken both during the day and night at all the sites except for MD(4) (day samples only). Adult copepods caught by the 500- $\mu$ m net were all identified and counted in entire leg A samples, while they were counted in half of each sample of leg B, using a Motoda box as a splitting device, all adult copepods in the 1/8 or 1/16th fractions taken from the 200- $\mu$ m net samples were identified and counted, according to their abundance, in 1 to 5 different subsamples of 1/73 plankton volume, using a Dolfuss counting chamber. Copepodids were also counted and identified to the genus level.

Abundances were computed as number of individuals per cubic meter of filtered sea water. Some frequently used indices of population structure were calculated, the Shannon-Wiener diversity index ( $H'$ ), in bits per individual, and Pielou's evenness coefficient  $J' = H'/\log_2(S)$  (where  $S$  is the number of species observed in a sample).

As the number  $N$  of individuals counted in the subsamples varies nearly two orders of magnitude across the plankton samples, it influences strongly the structure coefficients values. It is well known that the number of species found in a sample is a biased estimator of the species richness of a community. Accordingly, evenness and diversity indexes are assumed to be biased (Sheldon, 1969; Routledge, 1980; Rejmanek *et al.*, 1985; Soetaert & Heip, 1990, and many others). In order to correct the sampling effect of species richness bias, special procedures could be used, for example rarefaction or resampling statistical methods. We chose here to model the relationship between either  $S$  and  $J'$  versus  $N$ , using suitable empirical semilogarithmic functions fitted with our whole data set. More realistic functions including asymptote parameter estimation were unnecessary in the present context of low  $N$  values. The residual variability of  $S$  and  $J'$  was assumed to reflect the effect of the environment on population structure.

For species richness, the least squares fitted Gleason's law (see Tokeshi, 1993, for general comment on the topic) was as follows:

$$S = 9.04\log(N) - 0.08 \quad (1)$$

$$(n = 100, r = 0.727, p < 0.0001).$$

For  $J'$ , two far outliers were removed (samples 28c and 390c, 500  $\mu$ m net), leading to:

$$J' = -0.28\log(N) + 1.30 \quad (2)$$

$$(n = 98, r = 0.793, p < 0.0001).$$

In both cases the residual values were nicely homoscedastic and normally distributed within net.

Standardization of  $S$  and  $J'$  was then achieved by adding the residual value of each sample to the estimated value for  $N=100$  individuals. For example we compute:

$$Ss_i = S_i - f(n_i) + f(100), \quad (3)$$

where  $f()$  refers to equation (1),  $Ss_i$  is the standardized estimate of the species richness,  $S_i$  the raw species number in the  $i$ th sample and  $n_i$  the number of individuals. Last, the standardized diversity of each sample was computed as the product of the standardized evenness by the logarithm of the standardized richness, with an added covariance term (Welsh *et al.*, 1988):

$$Hs'_i = Js'_i \cdot \log_2(Ss_i) + cov(Js', \log_2(Ss)) \quad (4)$$

Covariance between  $Js'$  and  $\log_2(Ss)$  was found equal to 0.009.

As a result, some among-sites non-significant ANOVA tests computed for the raw coefficient values turned out to be significant when performed for standardized coefficients. Possible influences of the time of day (night samples compared to daytime samples), depth level, and sites on copepod abundance and standardized structure indexes were investigated by repeated measures of analysis of variance, taking advantage of the matched 500  $\mu$ m and 200  $\mu$ m samples for each haul.

Data from each sample are also presented using rank-frequency diagrams, RFDs (Frontier, 1976, 1985). For each site, the mean and the standard deviation (SD) of the log-transformed relative abundance were calculated for each rank. Then 'mean RFDs' were plotted with the corresponding curves for SD (Safran, 1987; Frontier & Etienne, 1990).

## Results

The copepods encountered comprised 91 species in 32 genera and 26 families. The full species list will be included in another paper (in preparation). The 500- $\mu\text{m}$  net collected mainly large copepods, of which the families present in the largest numbers were the Metridiidae (*Pleuromamma* spp.), Calanidae, Eucalanidae and Euchaetidae. Although in low abundance, the Sapphirinidae (associates of salps) were represented by 13 species. At no site did total average adult copepod abundance exceed 50 individuals/ $\text{m}^3$  in the upper 200 m water column. The 200- $\mu\text{m}$  net collected smaller species, including mainly the Clausocalanidae, Paracalanidae, Acartiidae, Oithonidae and Oncaeiidae; the total copepod abundance was between 1000 and 5000 individuals  $\text{m}^3$ . We did not treat the 80 $\mu\text{m}$ -net samples, which were processed by Thibault *et al.* (1994), especially to estimate nauplii: adult ratios.

Furnestin *et al.* (1966) and Furnestin (1979) recognise 31 copepod species as being at present transported practically continuously from the Atlantic into the Mediterranean. Giron (1963), as well as Mazza (1967), Duran (1970), and Seguin (1972) mention 21 species as of Atlantic origin. In the present study, ten of these 31 species were taken in the Atlantic current Leg-A, RIJ(1) and LIJ(5): *Calanus tenuicornis*, *Calanus robustior*, *Calanoides carinatus*, *Calocalanus styliremis*, *Pleuromamma abdominalis*, *Pleuromamma borealis*, *Centropages chierchiae*, *Lucicutia flavicornis*, *Candacia bipinnata* and *Pontellina plumata*. All these species except three are at present widely distributed in the north-western Mediterranean, as shown in TOMOFRONT samples (Seguin & Dallot, 1989). They were not found in the present survey outside the Atlantic current sites, except for *C. chierchiae*, taken in small numbers at MD(4), and *Pleuromamma borealis*, abundant only at MAG(3).

Maximum copepod abundances were encountered at ADJ(6). At this site, sampled by eight hauls at four stations, the 500- $\mu\text{m}$  samples were overwhelmingly dominated by *Eucalanus elongatus* (77% of the total copepods in haul 431a). The most abundant species in this category (in decreasing order of abundance) were: *Eucalanus elongatus*, *Pleuromamma borealis* and *Pleuromamma abdominalis*. *Calanoides carinatus*, a species characteristic of the Atlantic current, was also present. In the 200- $\mu\text{m}$  hauls the most abundant copepods were the Clausocalanidae, particularly *Clausocalanus arcuicornis* and *C. furcatus*, as well as small copepods such as the Oncaeiidae (*Oncaea dentipes*),

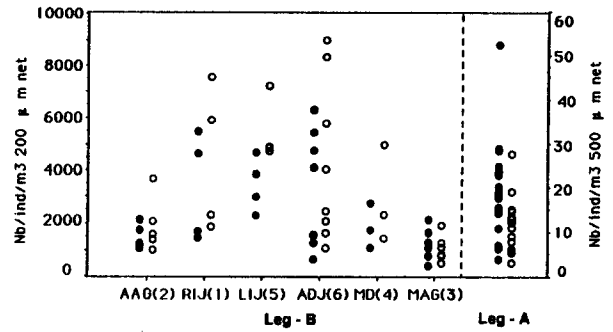


Fig. 2. Total copepod abundance in number of individuals  $\text{m}^3$  for each haul at the different legs and sites. Open circles: 500  $\mu\text{m}$  samples, closed circles: 200  $\mu\text{m}$  samples.

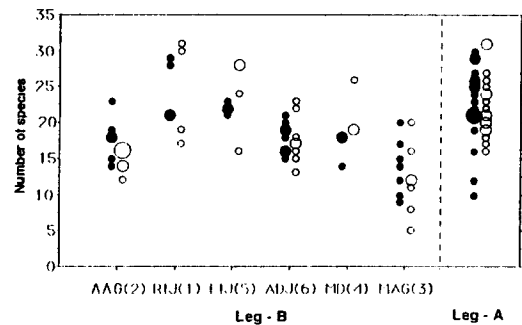


Fig. 3. Copepod species richness for each haul at the different legs and sites. Symbols as in Fig. 2. Circle diameters are proportional to the number of samples having the same species number.

the Oithonidae (*Oithona helgolandica*) and the Acartiidae (*Acartia clausi*). The sites of greatest abundance were LIJ(5) and RIJ(1). In the 500- $\mu\text{m}$  net samples at the former site, the following species were constantly dominant: *Eucalanus elongatus*, *Calanus helgolandicus*, *Pleuromamma borealis* and *Rhincalanus nasutus*. In the 200- $\mu\text{m}$  samples, a great abundance of Clausocalanidae was taken, followed by the Oithonidae. At site RIJ(1), the 500- $\mu\text{m}$  net sampled high numbers of large copepods, particularly: *Temora stylifera*, *Pleuromamma abdominalis*, *P. borealis*, *Eucalanus elongatus* and *Calanus helgolandicus*. In the 200- $\mu\text{m}$  samples the more abundant species belong to the Clausocalanidae, the Oncaeiidae and the Oithonidae. Sites AAG(2) and MD(4), however, showed lower values. The Mediterranean water, MAG(3), showed the lowest abundance and species numbers with both mesh sizes. *Pleuromamma abdominalis*, the most abundant of the largest species, outnumbered the Clausocalanidae, Oncaeiidae and Oithonidae.

Paired *t* tests performed on the whole data set demonstrated highly significant differences between the 500  $\mu\text{m}$  and the 200  $\mu\text{m}$  mesh size nets. The abun-

dance ratio from 200  $\mu\text{m}$  to 500  $\mu\text{m}$  net was around 300. The 500  $\mu\text{m}$  net caught more species (mean difference and standard error  $1.9 \pm 0.7$  species,  $p = 0.0059$ , not the case for leg-B alone, see below) and these samples showed highest evenness ( $0.07 \pm 0.02$ ,  $p < 0.0001$ ) and species diversity ( $0.43 \pm 0.09$ ,  $p < 0.0001$ ). Nevertheless, both nets gave coherent results for both abundance values and number of species identified in the subsamples (Figs 2, 3). From leg B alone, using the structure index values, no significant interaction between site and net type was found (Table 1). Numerical abundance and species number show a pattern similar to that for biomass (Thibault *et al.*, 1994). Abundance was highest in the mesotrophic Atlantic current and very low in the distinctly oligotrophic Mediterranean water and in the southern Atlantic water gyre. Copepod abundance varied differently in both nets from leg A to leg B. An ANOVA test, computed on the log-transformed number of individuals per cubic meter, leads to rejection of the hypothesis of no interaction between net type and leg, with a 0.019 associated probability. The copepods caught in the 500  $\mu\text{m}$  net increased from  $9.7 \pm 1.4$  (mean  $\pm$  SE)  $\text{ind}/\text{m}^3$  in leg A to  $17.6 \pm 2.6$   $\text{ind}/\text{m}^3$  in leg B. The contrary was observed in the 200  $\mu\text{m}$  samples, in which the numbers of copepods decreased from  $3172 \pm 435$   $\text{ind}/\text{m}^3$  to  $2378 \pm 282$   $\text{ind}/\text{m}^3$ . It was not possible to choose between the influence of different hydrological compartments in which the stations were located during the two legs or to a seasonal effect (i.e. an increasing sea water temperature during the cruise).

The day/night effect was significant for abundance in both nets, as usual, but this was not observed either for the standardised richness or for evenness and species diversity. Effects of depth layer (a, b or c hauls), or depth versus time-of-day interaction, were never significant. This result may result from a type II statistical error, or population mixing and entrainment within the 200 m upper layer of the jet stations. This phenomenon was substantiated by the chlorophyll 'a' vertical distribution, which, in some case, exhibited a deep secondary maximum (sites 1 and 5). In one case, as observed in the Liguro-provençal frontal zone, the vertical distribution of the copepod population could have changed (Dallot & Seguin, 1992). For this reason we did not pool the a and b sample counts in the following statistical treatments, in order to compare them to type c sample counts, and used all the data, whatever their depth origin.

Between-sites differences in standardised species richness (Table 1) were significant for both nets and

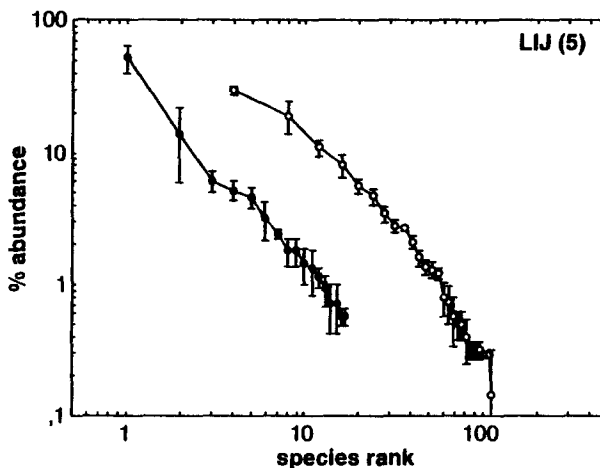


Fig. 4. Mean-RFDs and standard deviations in the jet, LIJ(5) site, for the 200 (closed circles) and 500  $\mu\text{m}$ -net samples (open circles, shifted to the right, ranks  $\times 2$ ).

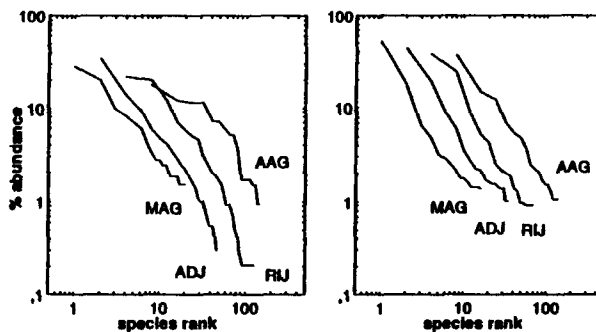


Fig. 5. Mean-RFDs for sites MAG(3), ADJ(6), RIJ(1) and some samples (station 380) of AAG(2). Left side: 500  $\mu\text{m}$ -net samples; right side: 200  $\mu\text{m}$ -net samples. The RFDs of the different sites are successively shifted to the right as in Fig. 4.

not significant between type of net. The highest values occurred at the Atlantic current sites RIJ(1) and LIJ(5) and the lowest at the Mediterranean gyre and Atlantic divergence site. MD(4) and AAG(2) showed intermediate values. The between-site ordering of evenness and species diversity values was identical to those observed for species richness. Some stations of Leg A located in the Mediterranean anticyclonic gyre rim and in the jet were compared to MAG(3) and to grouped Atlantic jet sites. No significant difference was found for any structure indexes and abundance values. In Leg-A, some high abundance values were encountered within the Mediterranean anticyclonic gyre and near the northern cyclonic eddy (station 36), the lowest values corresponding to the coastal Spanish stations near Cartagena. The comparison between Leg-A and Leg-B figures could not be pursued any further because of

Table 1. Leg B results. Mean and standard errors of log-transformed copepod abundance (either net) and structure index values (averages of both nets) for each site, and corresponding repeated-measure ANOVA-associated probabilities.

Descriptors:	Copepod abundance log (n/m <sup>3</sup> )		Standardized structure indicators		
	500 $\mu$ m net	200 $\mu$ m net	Richness Ss	Evenness Js'	Diversity Hs'
Sites:					
Atlantic water anticyclonic gyre AAG(2)	1.04 $\pm$ 0.18	3.14 $\pm$ 0.07	17.6 $\pm$ 0.9	0.75 $\pm$ 0.02	3.08 $\pm$ 0.12
Jet: right inside RIJ(1)	1.51 $\pm$ 0.09	3.47 $\pm$ 0.14	21.8 $\pm$ 0.9	0.80 $\pm$ 0.02	3.56 $\pm$ 0.12
Jet: left inside LIJ(5)	1.44 $\pm$ 0.01	3.42 $\pm$ 0.06	19.2 $\pm$ 1.0	0.80 $\pm$ 0.03	3.40 $\pm$ 0.15
Jet: atlantic divergence ADJ(6)	1.67 $\pm$ 0.08	3.50 $\pm$ 0.03	16.7 $\pm$ 0.6	0.71 $\pm$ 0.03	2.88 $\pm$ 0.14
Mediterranean water divergence MD(4)	1.33 $\pm$ 0.23	3.30 $\pm$ 0.14	18.9 $\pm$ 1.4	0.76 $\pm$ 0.03	3.24 $\pm$ 0.16
Mediterranean water anticyclonic gyre MAG(3)	0.79 $\pm$ 0.16	3.06 $\pm$ 0.08	15.6 $\pm$ 0.8	0.70 $\pm$ 0.03	2.79 $\pm$ 0.14
Repeated measures Anova probabilities:					
between sites	0.0003		0.0053	0.0172	0.0046
between net types	0.0001		0.21	0.0004	0.0005
interaction	0.56		0.31	0.35	0.24

poorly characterised hydrobiological conditions and lack of replication of the stations from Leg-A.

The Rank-Frequency Diagrams (RFD) matched pairs, as they were established separately on the 500  $\mu$ m and 200  $\mu$ m sample counts, show characteristic differences in shape (Figs 4 and 5). The 500  $\mu$ m samples are more convex and more extended to the right than their 200  $\mu$ m duplicates, which are more frequently linear and even concave. Such a features are linked to the evenness and richness significant differences which we have shown previously. There was little difference between either depth-type *a* or *b* hauls, and also little difference between day-time and night-time hauls. A good representation of the form and the variation of the RFDs at each site is given by drawing the mean relative abundance for each rank and the envelope corresponding to  $\pm$  one between-sample standard deviation (Fig. 4). Most of the curves from the stations at each given site remain within a narrow band, around the general shape characteristic of that site. Site AAG(2) was an exception in that the 500  $\mu$ m RFDs samples fall into two distinct subgroups of different shapes: linear (stations 376 and 378) or markedly convex (station 380).

The RFDs shape could be used to characterise the ecological succession stages represented by the species assemblages sampled, according to the Margalef-Frontier theory of ecological succession, Frontier 1976, 1985. Stage 1, the 'pioneer stage' is concave towards the top, because of some highly dominant species. Such a figure is observed in the 200  $\mu$ m samples of the within-jet site 5. RFDs become linear or

slightly convex, indicating a stage 1' in most of the other sites. A tendency to more pronounced mature stages 2 or 3, characterised by more or less pronounced convexity and increasing number of species, is observed principally in the 500  $\mu$ m samples (Fig. 5). Exceptions include station 380, AAG(2), a mature community with dominant species of similar abundance as well as stations at the sites MAG and RIJ, where the RFDs show a series of steps. These steps usually are interpreted as resulting from mixing of populations of different origins.

By contrast, the RFDs for the 200- $\mu$ m samples are all similar, linearly decreasing and can be all included in succession stage 1' (Fig. 5, right). A slight concavity appears in the jet and MAG samples, suggesting either a juvenile system or a mixture of populations. A very high similarity in the respective abundances of the two dominant species, characteristic of development towards stage 2, can be seen at site AAG(2).

## Discussion and conclusions

The interpretation of species abundance patterns generally follows niche-oriented or statistically-oriented model points of view (Tokeshi, 1993). These classical approaches are hard to manage in practice because of frequently encountered interpretative or fitting difficulties which then lead to overall ambiguous model identification. We choose to refer to the Margalef-Frontier empirical frame of succession process within

a community (Margalef, 1957; Frontier, 1985). In their view, characteristic chronological changes of structure index values and species abundance patterns (RFD) could be reliably observed in marine and freshwater communities under the influence of transient disturbing events. In the open sea, and primarily in ergocline areas like fronts, such events occur at particular places which correspond to the 3-dimensional organization of the hydrological structures. They refer to physical-biological interactions such as the effects of water mixing on pelagic production outburst or behavioural species swimming response to cross frontal circulation processes (Boucher, 1984, 1988; Olson & Backus, 1985).

This paper is mainly based on the speculative value of community structure indices and species abundance diagrams to draw inferences about the succession stage of a community. Some problems arise from the small amount of sea water filtered by each haul (i.e. 25 or 50 m<sup>3</sup>) and the influence of the size of the subsamples on the computed values. Standardization of the structure indexes leads to more satisfactory among-site comparisons, but it does not resolve the bias problem. Similarly, a RFD directly drawn from the counts will not necessarily be an accurate view of the community pattern. To date, RFD standardization remains unresolved.

Numerous authors have related zooplankton diversity to pelagic environmental conditions. For example Longhurst (1967) showed that in the California Current, the number of species per plankton sample aliquot is highest in areas of mixing of different ecosystems by advective processes or by vertical superposition of water masses of different origin. In the California coastal upwelling zone, the species diversity is low (like high latitude plankton communities) and the species dominance is high and linked to increased biomass. A similar situation was observed by Binet (1970) in regard to the copepod communities in the Benguela current frontal zone which is also dominated by coastal upwelling. In Mediterranean coastal waters, Seguin (1981) and Lakkis (1990) showed that minimum Shannon index values are characteristic of spring and summer periods of maximum copepod abundance. In offshore areas of the Indian and Pacific oceans, Timonin (1971) and Gueredrat (1971) corroborated the overall low Shannon diversity index values associated with divergence zones; the contrary is true of stratified waters or convergence zones. More recent studies of copepod populations across and along frontal structures have focused on selected species or species

group distributions and have neglected to discuss both structure index values and ecological succession stages (Ashjian, 1993; Ashjian & Wishner, 1993).

In the present study, the positive trophic effects of the frontal structure are clearly seen in mesozooplankton biomass (Thibault *et al.*, 1994) and copepod abundance. The general region of the Atlantic water front appears to show the highest copepod abundance within the study area. The maximum abundance of the smallest species (mainly caught by the 200- $\mu$ m net) is observed on the left edge of the Atlantic current, decreasing progressively towards the Anticyclonic Gyre to the south. Large copepods (500- $\mu$ m hauls) are most abundant in the jet. For the 200- $\mu$ m samples, this corresponds to a six-fold difference in abundance between the Mediterranean site (the poorest), and the left edge of the jet (the richest). For the 500- $\mu$ m samples, the LIJ(5) samples were eight times as rich as MAG(3). It is probable that secondary production is exported from sites ADJ(6) and LIJ(5), regions of high copepod abundance and 'young' population structures, across the Atlantic current, RIJ(1), towards site AAG(2), a region of low abundance and mature structure. Thibault *et al.*, 1994, showed low O:N ratio for copepod assemblages in site AAG2 (O<sub>2</sub> respiration versus N-NH<sub>4</sub> excretion) characteristic of a carnivorous feeding regime. This suggests that a transfer of material progressively takes place within the trophic network towards those species showing high biomass and those with the longest lifetimes. This transfer corresponds also to one across the Atlantic current from north to south. The observed pattern of variation of the structure indexes and changing shapes of RFDs lead to compatible conclusions. Diversity is high in the Atlantic current, particularly after it leaves the frontal region, where Mediterranean assemblages are mixed with those transported eastwards from the Atlantic Ocean. An active divergence zone within the jet takes place at site 6 with high autotrophic carbon fixation (1835 mg Cm<sup>-2</sup>d<sup>-1</sup>), Videau *et al.* (1994). Such a situation is linked to low structure index values, as generally found in the literature. However at site MD(4), characterised by an unproductive hydrological divergence of Mediterranean water, the structure index values remain high, conclusively indicating the dominant influence of the productivity level on the ecosystem structure. In the jet, the change to a high level of secondary productivity is distinguished by an increase in dominance by the principal copepod species and a corresponding reduction in evenness: concave or linear RFDs, more pronounced in the 200  $\mu$ m samples, which

include mainly small short-lived species. This is most marked at the Atlantic divergence site ADJ(6), where the small copepod species show their maximum abundance and where large species assemblages are dominated by patches of *Eucalanus elongatus*. The abundance of the largest copepod species, as well as overall species richness, evenness and diversity increase from the left part to the right part of the jet, corroborating that the direction of succession (from juvenile to mature stage) within the copepod community conforms to the direction of the secondary circulation flow. The heterogeneous conditions observed within the Atlantic anticyclonic gyre populations (stage 2 RFD mixed to 1') may be linked to episodic population and food transfer coming from the jet. Otherwise, the structure indexes and biomass are lowered. Such a situation was also encountered within the Mediterranean anticyclonic gyre. This probably agrees with the so-called degenerative stage 3 of succession with unsustainable high production within gyres (Frontier, 1985).

While the indices of population structure and the RFDs show significant contrasts among sites, the high frequency of stage 1' RFDs and their constancy of shape across the whole sampling zone are striking. This particularity has already been described for carnivorous gelatinous macroplankton from the Alboran Sea (Dallot *et al.*, 1988). This may be interpreted as a consequence of the recurrent high planktonic production in a wide region under the influence of the Atlantic front. Lateral displacements and meanders of the current may influence a region much more extensive than that of the current itself. The gyres, by contrast, tens of km in extent, probably last in excess of several weeks, even months, a period longer than copepod generation times, which would give time to progressively modify the abundance and the structure of their mesozooplankton populations under more pronounced oligotrophic conditions.

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